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THE AGGREGATE ORIGINATION OF PARASITIC PLANTS

DR. CHARLES A. WHITE

SMITHSONIAN INSTITUTION

IN the January number of THE NATURALIST I gave a review of the known phenogamous parasites, in which was discussed the relation of the parasites to one another, and to other abnormal plants; and the relation of all of them to normal plants. The present article is devoted mainly to the question of the manner of origination of the parasites as such, which, it is assumed, was by abnormal aggregate mutation from normal phenogams.

Parasitism in the animal kingdom is perpetrated by low, upon higher, forms of life, the parasites belonging to families, orders and even to classes, which are widely different from any of those which include the hosts. Parasitism of low forms of vegetable life upon higher forms is also everywhere prevalent, such as that of fungoid cryptogams upon phenogams, but the cases now under consideration are those of parasitism of various kinds of phenogamous plants upon other phenogams. Evidence of this phylogenetic relationship of parasites and their hosts, even in extreme cases of parasitic deformation, is fortunately preserved in that part of the structure of the parasites which pertains to parturital reproduction. That is, the florescence and fruitage of the parasites have remained characteristically phenogamous, each parasitic species having preserved at least those floral and pericarpal structures which normally characterize the phenogamous families, as such. It is thus observable that, in the abnormal mutation which produced the parasites, the effect was chiefly confined to the somatic parts of the respective plants and to those parts which are concerned in blastemal reproduction; while the parts immediately concerned in systematic genesis by parturital reproduction were, at most, only slightly disturbed. So distinctly are the systematic characters of normal phenogams retained in the florescence and fruitage of the parasites that one seems forced to the conclusion that, in the great systematic development of vegetal forms, they all became phenogams before they became parasites. The phenogamous parasites, therefore, not only do not belong to a separate and predatory class, as is the case with other parasites, but they are depraved members of the same class, and sometimes of the same family, with their hosts. Still, their depravity is only with reference to the habits and structure of normal plants, for they all have great adaptability to their peculiar conditions, and their vegetal vigor is quite as great as is that of normal plants.

It is a fact worthy of special attention in this connection that although all the various forms of phenogamous parasitism are accompanied by greater or less abnormality of structure, they are in certain respects subject to the systematic restrictions which pertain to normal plants. That is, each form of parasitism affects not merely certain individual members of a given species, but every member of it; and the systematic limits of that species are, for itself, the limits of its own peculiar form of parasitism. Moreover, that form of parasitism which characterizes each of the different groups is shared without variation by every member of the group regardless of the generic or family relationship which it may bear to other plants. The habits and other parasitic characters of those depraved phenogams are as distinctly and permanently heritable as are the stated specific, and other systematic, characters of the same, or of any other, species, and there is no known evidence that any form of phenogamous parasitism has been derived by transmutation from any other parasitic form. Known evidence tends to show that every case of such parasitism originated independently of all other cases, and by a mutative process which imposed permanent abnormal characters upon normal plants. Those abnormal characters all became connate with the normal characters after the establishment of their heredity, but they never became systematically correlated with them.

The questions that here almost crowd themselves upon one's attention are, how have those wayward phenogams accomplished their departures from normal conditions, and what was their incentive for doing so? Doubtless in all cases the chief incentive to parasitism, after the operation of an unknown predeterminate cause, has been food-lust, the instinctive object of the plant being to procure its nourishment in an immediately available form. The following respective references to the seven groups of phenogamous parasites are necessary to the present subject, but they show how difficult it is to make any sufficient answer to the first of those questions.

In pursuance of the subject as just indicated it may be suggested that the members of group I, which prey upon the roots of other plants and are only partially parasitic, originally acquired their habit of underground pilfering by the accidental chafing together of the tender roots of closely-growing plants, which brought bared, new-formed cells into contact at the crossings of the roots. Vital union of the roots at those points, such as takes place in grafting, having resulted, the more vigorous plant became the parasite by withdrawing a portion of the partly elaborated food-sap from the weaker one. It is plain, however, that thousands of cases are constantly occurring of similar contact of growing roots which do not result in parasitism. Both the normal and abnormal characters are possessed by every individual plant of every species pertaining to group I, and they are thus, all to the same extent, distinguished from normal plants and from all other parasites. In no case is one of this simplest of the forms of phenogamous parasitism known to show any inclination to greater complexity, or to abandon its present restricted parasitic habit. The heredity of that habit is permanent, and no known fact suggests that it originated by any slow process, such as is generally understood to be the case in natural selection.

The mistletoes, which represent group II, have reached the condition of complete parasitism with less structural and functional change than have any of the other recognized groups. In view of the fact that they produce their own chlorophyl, and that their structure is very nearly normal, one can not doubt that they were originally normal phenogams, growing from the soil, although they will not now grow there. As a family also, they are now quite distinct from all other families, and as a group of parasites they are so clearly separate from every other group that one can not doubt that they have reached their parasitic condition in an entirely different manner. Their departure from the life-habit of normal phenogams evidently consisted only of the transference of germination and epitropism from the soil to the bark of trees; while the epitropic structure and functions, including both parturital and blastemal reproduction remained normal. Unnatural and lacking in apparent incentive as has been that transference, it is believed to have been suddenly accomplished for the whole family, no trace of transitional stages of parasitism having been discovered for the species of either the Old World or the New. Although the mistletoes are so nearly normal in structure, their parasitism is as complete and heritable as is that of any of the other groups.

The European species, *Lathræa squamaria,* which has been chosen to represent group III, besides being distinct from all other known parasitic forms, is, in a peculiar manner, suggestive of the assumed suddenness with which changes from normal to parasitic conditions have occurred among phenogams. This species has five distinct abnormal habitudes, which are repeated in succession in every individual plant. Its germination is from an ordinary seed in surface soil, and it is developed as a normal plantlet from a normal embryo; but it soon abandons itself to a remarkably diversified life. First, it produces sessile haustoria upon some of its early roots and becomes partly parasitic in the same manner as do the members of group I, the structure and habit of which it then closely resembles. Second, it resorts bodily and suddenly to underground life by burrowing into the soil, where it becomes an intricate mass, often very large, of blanched stems and branches. Third, it abandons its early roots with their sessile haustoria, develops new pediculate haustoria from its underground stem and branches and becomes completely parasitic. Fourth, it changes some of its numerous aborted leaves into ingenious traps with which it captures minute animal forms and adds them to its other ill-gotten subsistence. Fifth, almost suggestive of atonement for a groveling life, it provides for the normal germination of its offspring by sending above ground a few specialized branches which produce perfect flowers and seed and then die, while the underground parts live perennially. That series of changes of structure and habitude within the life-history of a single plant has no known parallel in the vegetable kingdom. The changes have no apparent relevancy with one another until the closing one of the series, parturital reproduction, restores the normal phenogamous condition for a new reproductive cycle and a new series of the abnormal changes. All these changes of structure and habitude are invariable in character and invariably heritable. So far as is now known they are confined to a single species, and the structure of no other known plant offers any suggestion of their gradual origination. In view of such facts as these, all of which have been attested by competent observers, one may reasonably believe that not only this form, but all the forms of phenogamous parasites, have originated suddenly.

Although groups I, II and III are, by their respective methods of parasitism, clearly distinct from one another and from normal plants, parasitism is not physically manifested in any of them until after germination is completed, because the embryo of every member of each of those groups is of normal structure. Every member of the four remaining groups, however, begins life in an embryo which is simple and filiform and without cotyledons, radicle and plumule, although the flower in which it is produced is of normal phenogamous structure. Moreover, although the simple abnormal embryo is physically identical for each of the four groups just mentioned, the resulting forms of parasitism are too widely different for each group to suggest for them even a remote community of origin.

A remarkable fact concerning group IV is that the two genera which compose it, Cuscuta and Cassytha, belong to widely different families, namely, Convolvulaceæ and Lauraceæ, respectively, and that the respective genera prevail in distantly separated parts of the world. Both genera are endowed with a single parasitic impress which distinguishes and dominates them equally in both habitude and somatic structure. That impress also separates all the species and individual plants of the whole group from normal plants and from all other parasites. The habits of this group, as shown by our well-known dodders, are widely different from those of all the other parasitic groups. They are all annual plants and consequently the whole life history of each species is crowded into a single season, which is shortened by late spring germination and early frosts. Therefore all the characteristics of the whole group lie dormant in the simple filiform embryo of every dodder seed for more than half of each year; and yet every one of those characteristics is invariably heritable and constant. Difficult as it is to understand how every individual member of such a distinctly defined double group of annual plants could have assumed their abnormal characteristics either slowly or suddenly, and attained a world-wide distribution, it is still more difficult to understand how two such diverse genera could have assumed identical parasitic characters. It is almost superfluous to add that the habits and structure of no known plant offers any suggestion of a gradual origination of the parasitic characters of group IV, or of the manner of its world-wide distribution.

As is the case with the other groups which are herein mentioned, nothing is known of the pre-germinative history of the characteristics of group V. The members of this group belong to a noted family of parasitic genera, the Orobancheæ, of which the destructive broom-rapes are among the best known examples. They all begin life in a simple, filiform embryo, which is not only without differentiation into cotyledons, radicle and plumule, but which is also extremely abnormal in its method of germination. The members of group V, like those of group IV, are annuals. As regards the structure of the seed and embryo and the initial conditions of germination, the members of both groups are similar, but their results are extremely different. The germinating offshoot of the former springs upward, sending no root into the ground, but seizing upon the growing parts of its companion plants by its haustoria. The offshoot of the latter burrows downward and seeks a root-host, failing to find which it dies without producing any upward growth. Finding a root-host, a substituent plantlet is developed from their conjoined parts which rises above ground, producing flowers and seed. The physical structure of the embryo of both plants is identical, and both are abnormal. Immediately upon germination the great differences between the plants appear, but neither in those differences or in their common embryonal structure is there any suggestion of a community of origin with each other, or with any other plants.

A leading characteristic of all the forms of phenogamous parasitism is the permanence and heredity of their attributes. Increasing abnormality of structure and habit, however, is suggested, but not proved, by the members of group VI, which is represented by the Rafflesias and some closely related genera. The conception which one naturally forms of a phenogam that may have been the normal ancestor of these plants is one having root, stem, branches, leaves, flowers and fruit. These plants have discarded most of those essential parts, none of them having more than a short stem besides the fertile flower; and the sessile species, which are numerous, retain only the flower. Such a conception would therefore carry with it the idea that those eliminations were consecutively effected until the lowest structural limit was reached; but neither their own structure nor that of any other known plants affords the least indication that any of these parasites reached their present condition by either selective gradation of successive steps. The Rafflesias, like the mistletoes, are parasitic upon trees, and the seeds of both will not germinate successfully upon the ground. One may well believe that when the mistletoes abandoned the soil and inflicted themselves upon trees they took with them, and retained, all that they then needed for their support. But when the Rafflesias made their similar change, as they are assumed to have done, they required from their hosts the fullest possible tribute. Apparently sure of receiving it, they discarded as no longer necessary the principal part of their own somatic and blastemal structures, the sessile species retaining only those parts which are concerned in parturital reproduction, namely, only the flower. Their success has been complete, for although they are rootless, stemless, branchless and leafless plants, and originate from a structureless embryo, they are among the most vigorous of vegetable forms, the flower of the largest species sometimes reaching a diameter of more than three feet. One cannot conceive of a wider departure from normal conditions than is presented by group VI, or of a more complete isolation of structure and habit from all other plants.

Group VII, which is represented by the Balanophoreæ, is remarkable for the comparatively large number of systematic genera which it embraces, some of which are so greatly differentiated from others as to deserve recognition as sub-families. Some are comparatively inconspicuous; some produce large, showy flowers, and some bear an outward resemblance to fungi, to which early botanists referred them. The genera of this group are still further distinguished by the comparatively small number of species which represent them, the average number to the genus being less than three. Yet all the members of this remarkably diversified group are developed from a simple filiform embryo by a germination similar to that of the broom-rapes, and all are rigidly controlled by one invariable and heritable method of parasitism. It is almost superfluous to add that there are no known intermediate forms between the parasitic species of this group, or between them and normal phenogams.

A leading purpose in the foregoing remarks is to express the belief and present evidence that all the various methods, or forms, of phenogamous parasitism have originated suddenly by abnormal mutation from normal phenogams and that each form originated independently of all the others. One can not doubt that, whatever may be the determinate cause, all mutations of plants, whether normal or abnormal, originated in changes of molecular conditions within the germ cell. Usually, those molecular changes are of phylogenetic character, but there is no reason to doubt that the changes which gave origin to the various parasitic attributes were also of like molecular origin. That is, referring to the theory of intracellular pangenesis of de Vries, each of those attributes, as well as their associated abnormalities of structure, both somatic and embryonic, had its origin in abnormal pangenes. Admitting such a community of molecular origin, there appears to be no more reason to doubt the origination of parasites by aggregate mutation than to doubt normal aggregate mutation.

One who accepts without qualification the theory of the origin of species by natural selection is no more likely to favor this idea of the sudden origination of the great and diverse groups of parasites which have been referred to in preceding paragraphs than he would be to accept the theory of special creation of species, belief in which was formerly universally held. But by those who have given due consideration to paleontological facts with regard to the evidently sudden introduction at various stages of geological time, not merely of species, but orders and classes of animals and plants;[1] to the great array of facts presented by Professor Hugo DeVries in support of his mutation theory;[2] to the cases of aggregate mutation of Lycopersicum which I have published from time to time as results of my personal observations;[3] and to like cases of aggregate mutation of *Gossypium* which have been observed by Dr. O. F. Cook,[4] the proposition that the different forms of phenogamous parasitism have been introduced separately and suddenly will not be hastily rejected. When the attention of one who holds the former of the two views referred to is called to the cases of evidently sudden introduction of animal and vegetable forms during geological time he usually replies by deploring the imperfection of the geological record, although he constantly depends upon it in the multitude of cases in which phylogenetic continuity is evident. And yet, there is no break in the geological record, which is more abrupt and differential than is that which exists between the distinguishing characters of the phenogamous parasites and the normal characters of every other phenogam now living contemporaneously with them.

Briefly reviewing the foregoing subject, we find as follows: (1) The parasites which have been discussed are known to be phenogamous by the character of their florescence and fruitage, but for this occasion they are classified by their parasitic differences only. They are divided into no less than seven distinct groups, or kinds, which differ in character from root pilfering by means of a few haustoria to dominant rapacity, extreme deformation of somatic and embryonal structure and aberrant methods of germination. (2) The method of parasitism of each group is shared equally by every member of it, whatever may be the systematic affinities of the respective members, and the method of each group is entirely unlike that of every other group. (3) All the parasitic habits and structures are severally and completely heritable, and always connate with systematic features of the species in which they occur, but they are never systematically correlated with them. (4) None of the seven forms of parasitism shows any tendency to return to normal conditions, to become more complex, or to change from one form to another. (5) The normal florescence and fruitage of the parasites is assumed to indicate that they were originally derived from normal phenogams; but no trace of intermediate stages between even the most extreme cases of parasitism and normal plants has been discovered. The geographical distribution of all the known kinds of phenogamous parasitism, except that of group III, is almost world-wide. In consideration of these, and many kindred, facts it is assumed that the phenogamous parasites originated as such by sudden and aggregate mutation from normal phenogams, similar to, but not identical with, the phylogenetic aggregate mutation that has been observed in Lycopersicum and Gossypium.

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[1] I have discussed these questions in Report of the Smithsonian Institution for 1901, pp. 631–640; *Bulletin Torrey Botanical Club*, New York, Vol. 29, pp. 511–522; Album der Naatur, Haarlem, April, 1903, pp. 231–238; Natur und Schule, Berlin and Leipzig, III Band, pp. 248–253; and *Science*, New York, Vol. XXII, n. s., pp. 105–113.

[2] Die Mutationstheorie, Leipzig, 1901.

[3] *Science*, n. s., Vol. XIV, pp. 841–844; *ibid.*, Vol. XVII, pp. 76–78. New York *Independent*, Oct. 16, 1902; *Bull. Torrey Bot. Club*, Vol. 29, pp. 511–522; *The Popular Science Monthly*, Vol. LXVII, June, 1905, pp. 151–161.

[4] *Proc. Washington Acad. Sci.*, Vol. VIII, p. 265; *Science*, n. s., XXVII, p. 193.